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The Center for the Study of Rhythmic Processes continued its work on Central Pattern Generators (CPGs), notably on the vertebrate spinal CPG for undulatory locomotion, and the invertebrate crustacean stomatogastric ganglion (STG). For the lamprey, a primitive vertebrate, experiments were designed and performed involving transduction of mechanical motion to neural activity; these experiments were combined with mathematical theory to help understand the relation of structure to function in that network. Other topics investigated included the effects of long coupling fibers, the relationship between muscle activation and movement, and the ability of the network to regenerate. Work on the STG included results on neuromodulators that change the output of the network and mathematical modelling of indiviual cells as well as emergent properties of the network.

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Activity Report 10/1/88– 12/31/39

During the third year of operation of the Center, we have continued to make substantial progress in both theoretical and experimental directions. We have been joined in our efforts by Dr. M. Remler (V.A. Medical Center, Martinez, associated with the University of California at Davis), Dr. J. Buchanan (Marquette University), Dr. Graham Bowtell (a mathematician at the Open University of London, England) and T. Kiemel, a graduate student in mathematics working in the lab of A. Cohen). A short description of the work on each of the main subprojects is given below.

I. Large networks and the lamprey central pattern generator

1. Mechanical forcing of the in vitro lamprey spinal cord. (Kopell, Ermentrout, Sigvardt, Williams and Remler

In a previous progress report, we discussed experiments on the in vitro spinal cord using local bending at one end of a piece of the cord. The mechanical signals are transduced to neural activity by mechanoreceptors in the cord, and these signals are propagated through the CPG by the interneurons. A mathematical theory was developed to answer the question of what could be inferred from such data. The theory is given in "On chains of oscillators forced at one end", by Kopell and Ermentrout. The application of the theory to a part of the data is given in "Forcing of coupled non–linear oscillators: studies of intersegmental coordination in the lamprey locomotor central pattern generator" by Williams et al. This paper deals with inferences that can be made, in the context of the general theory, from knowledge of the range of frequencies at which pieces of the cord can be entrained with forcing at the rostral or the caudal end of the piece. The work offers an explanation of the otherwise puzzling observation that the range of entrainment for caudal forcing includes the frequency of the unforced piece of cord, but for rostral forcing the range lies at or above the unforced frequency. The general theory suggests that this is an expected and robust consequence if the caudal to rostral coupling dominates the rostral to caudal coupling. This work was presented in posters at the 1989 Berlin meeting on Neurothology and the 1989 Society for Neurosciences meeting. The papers are now complete and they and the abstracts are enclosed with this report.

A further paper, in preparation, deals with inferences that can be made, again within this theory, from the measured phase–lags along the cord and lags between the angle of the mechanical forcing and the angle associated with the neural activity in a root close to the bending. The studies of Williams and Sigvart have shown that there is a window of "allowed" phase–coupling between activity and movement. This window is predicted by the mathematical theory. Furthermore, Sigvardt and Williams have shown that the phase relationships that occur in the intact swimming lamprey, when the feedback loop is not broken, fall within this window, thus confirming that the relationship between sensory feedback and imposed movement of the in vitro preparation corresponds to the relative timing of activation and movement in the intact swimming animal.

Further mathematical work in progress on this project concerns the possible role of the long fibers of the cord in the outcome of these experiments. The current theory detailed in "On chains of oscillators ..." deals only with local coupling, and it is important to understand how the inclusion of such fibers might change the inferences.

2. Long fibers and development (Kopell and Ermentrout)

A second subproject on which much progress has been made concerns the potential role of long fibers in development. It is thought that all vertebrates display a sequence of behaviors in very early development: at some early stage, the tadpole – like animal

undergoes simultaneous contractions of muscles along one side of the body, contractions that may or may not be rhythmic, giving rise to so-called "C-coils". At a somewhat later and rhythmic stage, the embryo displays an "S-wave" : the rostral and caudal halves of the cord become a half-cycle out of phase with one another. Still later, species which swim by undulation go on to develop travelling waves of mechanical activity. The C-coils can be adequately understood from the existence of electrotonic coupling that is either neurogenic or myogenic. The explanation of the S-waves and the transition to travelling waves is much less clear. Also unclear is why, in many species, the wavelength of the travelling wave is approximately one body length.

We have been investigating analytically how the behavior of a chain of oscillators changes when long distance coupling is added. We found that we could obtain "S-waves" from "C-coils" by adding long fibers to a chain originally coupled in a way that models electrotonic coupling. These long fibers originate at the rostral and caudal ends of the chain and terminate at or near the middle; the connections model inhibitory interactions. If the local and long-distance coupling are both strong enough, the oscillators near the middle of the chain stop oscillating, and the units on either side become a half-cycle out of phase with the other half, i.e., display "S-waves". Furthermore, if more long distance inhibitory fibers are added, this time from the center outward to the ends, the "S-wave" behavior can become unstable and give rise to travelling waves. These travelling waves have as wave-length the length of the cord, i.e., approximately the body length of the animal. The above work is quite preliminary, but already suggests testable mechanisms for a sequence of behaviors seen in development. We are continuing to develop the mathematical ideas in order to be able to guide potential experiments and look for alternative explanations.

The travelling waves produced by the mechanisms described above do not appear to be stable to all perturbations, and should disappear in a fictive preparation significantly smaller than the entire cord. Thus, it is of interest that in preliminary data from the lab of A.H. Cohen, phase lags in fictive preparation of ammocoetes (immature lampreys) do not appear to have travelling waves; rather, the measured lags between electrodes have been either approximately zero or a half-cycle. This is in contrast to fictive preparations of adult lampreys, in which the phase lag of approximately 1% per segment is maintained for cord pieces less than half the total size. (This behavior of adult animals was produced in our previous models.) We conjecture that the local synaptic interactions necessary to maintain phase lags stably, even after transection of long fibers, are "tuned up" at some time during development; we have created some models to show how this might be done, using feedback from the mechanics. If the ammocoete results turn out to be robust, this suggests that a change in the properties of the synaptic connections might occur near transformation, when the life-style of the lamprey also changes from crawling in mud to swimming freely.

3. Design of substructures (Ermentrout, Kopell)

In an earlier paper, "Oscillator death in systems of coupled neural oscillators", we showed that in common models of interactions between neural oscillators, two-way interactions by means of a single pulse per cycle could lead to cessation of the rhythmicity if the interaction is sufficiently strong. The sequel to that paper, revised and expanded during this year, is now complete and has been submitted for publication. The sequel, "Multiple pulse interactions and averaging in systems of coupled neural oscillators", shows that subnetworks can be designed to work properly as oscillators, even if the interaction of neighboring oscillators is strong. The central idea is that the oscillator unit can be a composite, with the internal connections designed so that the cells fire at different points in the cycle and interact with neighboring oscillators at several or more phase intervals per cycle (as one sees in the leech CPG). This turns out to yield a mechanism which strongly inhibits oscillator death and promotes normal phaselocking. It also helps provide and explanation of how it is possible for the lamprey cord to behave as a discrete chain of oscillators, even though it is not anatomically segmented. That is, if the oscillator units are

composites as above, the behavior of the chain appears, at least numerically, to remain the same even when the connections between the oscillators are as strong as the internal connections between the pieces of each oscillator, so that the distinction between intra–oscillator and inter–oscillator is blurred.

4. Long fibers and intersegmental coordination (Kiemel, Ermentrout, Kopell)

The early models of Kopell and Ermentrout and also of Cohen et al. dealt only with local (but not necessarilv nearest neighbor) interactions between oscillators. (See 2. above for recent work of Kopell and Ermentrout involving long fibers.) Kiemel has extended that work to consider the addition of long fibers in one direction between every pair of oscillators at a given fixed length (such as half the length of the chain). The interactions are chosen so that they are approximately "tuned" with the short–range interaction. That is, the phase lag that would be result from any of the short range coupling in either direction or the long range coupling acting alone are all approximately the same. Kiemel showed that if the long range coupling is in the same direction as the dominant short range coupling, then the phase lags produced by the whole system can deviate in a systematic way from those of a travelling wave; the former have substantial deviations at a distance from the ends of the chain corresponding to the length of the long–distance interaction. This provides one explanation of such data on phase lags found in the lab of Cohen and discussed in a previous report. If the long range coupling is in the opposite direction of the dominant short range coupling, then the localized disturbances from the travelling wave do not occur. This work shows that the dominance of the short range coupling has a large impact on the behavior of the chains in the presence of one way long–range interactions. A special case of this analysis produces behavior in which any pair of oscillators is approximately in synchrony or in antiphase, a situation reminiscent of the ammocoete data of Cohen reported above. The work will be part of the Ph.D thesis of Kiemel in Mathematics (Cornell, 1990.)

Ermentrout and Kopell are now working on chains with short range and long–range coupling in both directions, in unforced and forced chains.

5. Relationship between muscle activation and movement (Williams and Bowtell)

Williams and Bowtell have developed and analysed a model of the mechanisms of swimming in the lamprey, in which the body of the animal is modelled as a segmented visco–elastic structure, and the neural activation is included as a forcing function working in parallel with the elastic and viscous element in each segment. The hydromechanics of the water were not included in the model. It was thought that the viscoelastic parameters in the model might be adjusted in such a way as to account for the mechanical properties of the water. Mathematical analysis of the mechanical system led to a series of equations which could then be solved numerically. The activation function used in the numerical manipulation of the model was based on the known timing of neural activation in the swimming lamprey. The behavior of the model was very different form the swimming lamprey, however, in that the mechanical responses ocurred approximately as a standing wave rather than a travelling wave. They then wondered whether the exclusion of the fluid mechanical properties of the water might account for the discrepancy, so they did the simple experiment of placing an intact animal on a slippery bench, out of water, and recording the movement on a video tape. Indeed, the movements of the animal did not occur as a travelling wave, but rather as a standing wave. The result points out the importance of the fluid mechanical properties of the water in the occurrence of a mechanical travelling wave during swimming. A manuscript on this is in preparation.

6. The mathematics of free (unforced) mechanical chains (Laederich, Levi)

This work clarifies some of the mathematical aspects of the previous work. A paper, "Qualitative dynamics of planar chains" has been completed and is enclosed.

7. Optical recording from lamprey spinal cord (Cohen)

A new computer was utilized and a new programmer hired to get the software completed. The optical recording and analysis equipment is now completely running. On several occasions, Cohen and her associate Guan Li have optically recorded action potentials during stimulation of single axons. In addition, some recordings appear to include slower potentials which may be post–synaptic activiry. This is being further tested and is progressing well.

8. Ammocoete studies (Cohen)

The experimental data on the ammocoete "fictive swimming" reveal that the bursting in the larval cords is far less stable than the adult. It also has some peculiarities, such as switches from near–synchrony to near antiphase in roots 10 segments apart. This has been observed in several animals to date. The cords take a very long time to stabilize to bursting that is regular and phaselocked.

9. Regeneration Experiments on adult lampreys (Cohen)

A paper describing evidence for functional regeneration in the adult lamprey spinal cord following transection is enclosed. The fibers of the spinal cord can regenerate and restore some intersegmental coordination to the central pattern generator, as tested in the isolated cord preparation. However, this test does not successfully give regeneration in all animals.

Further studies of the data demosnstrated that although there was clearly functional activity by the regenerated fibers, in fact the regrowth produced dysfunction in the cord as a whole. In these experiments, the protocol included partial transections. At the time of testing, after first testing the cord for normal function with the undamaged fibers present, the formerly undamaged fibers were cut and the cord retested. The data from preparations with the undamaged fibers present revealed that in all but one case the bursting was less well regulated than in formerly unoperated cords. Thus, even though there were still healthy undamaged fibers which should have been capable of normal coordination, the cords were unable to regulate their bursting well. Control experiments on acute lesions suggest that the regenerates behave even less well then the preparations with acute lesions. Thus, the presence of the lesioned fibers was disturbing as well as contributing to regulation.

10. Related work (Sigvardt, Williams and Buchanan)

Work not supported by AFOSR directly related to the efforts of the Center.

i) Sigvardt is continuing her study of paired cell recordings in the lamprey spinal cord *in vitro*, investigating interneuronal connections involved in fictive locomotion. This very taxing work is necessary to identify the actual cells which constitute the central pattern generator for locomotion. This data is important to refine hypotheses about long range and short range interactions. This work is supported by NIH.

ii) The Center has been fortunate to add as a new member Dr. J. Buchanan of the Biology Department of Marquette University. Buchanan, who has previously worked with Grillner and with other members of the Center, is studying the involvement in the lamprey CPG of certain classes of cells previously identified tentatively as belonging to that CPG. He is also modelling some of the behavior using the known connections. Both the modelling and the data will be of great help to the rest of the Center. This work is supported by the NIH. Buchanan hopes to be able to start work on lamprey embryology as well.

ii) In collaboration with N. Curtin, Williams has been involved in studies of muscle physiology. They have used a preparation of isolated lamprey muscle to study the relationship between force development and the velocity of shortening or stretch of activated muscle. These studies have shown that the force developed during stretch is very much greater than that developed during shortening of the same magnitude. In the intact lamprey, the timing in the caudal half of the body is such that the muscle is being stretched during approximately half of its activation period. Thus, work is being done on the muscle during the activation period, using energy that must come from the rostral half of the body, and this suggests that high force in the caudal regions of the body is particularly important during swimming.

II. Crustacean ganglia and small networks

1. Single cell oscillators (Epstein, Bucholtz, Golowasch, Meyrand, Marder)

In collaboration with Epstein, Bucholtz and Golowasch are writing mathematical models that describe the behavior of isolated LP neurons from the crab stomatogastric ganglion (STG). These data have been presented at the Society for Neuroscience Meeting, in a book chapter, and are in the process of being written for publication.

In a previous paper, revised during the last year, Epstein and Marder provided models of some of the behavior of a cell similar to the pacemaker AB cell of the crustacian STG. In conjunction with the models of the LP cell, this provides a start for work on subnetworks of the STG.

Meyrand studied the activation of the myogenic rhthms of a shrimp muscle by FMRFamide–like peptides. He found that these peptices can transform a passive muscle and a neurogenic muscular system into an oscillatory one that acts myogenically . These data are in Meyrand and Marder (1989), enclosed.

2. Network Oscillators – experimental (Marder, Dickenson, Meyrand, Weimann

Dickenson has recently found that two peptides, RPCH and proctolin can reliable activate rhythmic cardiac sac behavior. Under some conditions the cardiac sac rhythm is transformed from one–phase rhythm in the presence of RPCH. These data are described in Dickenson and Marder (1989), enclosed. More recently, Dickenson Mecsas and Marder have shown that a fused rhythm is produced in which the cardiac sac and gastric activity are joined (submitted).

Meyrand and Weimann have been describing neurons that can "move" from one pattern generating circuit to another. ("Neurons that participate in several behaviors", Weimann. Meyrand and Marder, in Crustacean Pioneer Model Systems in Neurobiology, K. Wiese, ed, in press). This is a different view of how neural networks are organized and will be the subject of Mr. Weimann's Ph.D thesis. This work has been presented at several meetings.

3. Related work on small networks

More investigators have joined to work on issues related to the modelling of crustacean neural networks, and a spinoff group from the Center has been formed, directed by Marder. The group includes Kopell, Epstein and two new people, L. Abbott of the Brandeis Physics Dept., and T. Kepler, a Ph.D. student of Abbott who is now doing a post–doc in the Marder lab. This work is not supported directly by the Center grant, but has been inspired by the Center, and has contributed directly to the thinking of Center personnel, such as Kopell. Abbott produced a mechanism to explain how the phase lag

between an oscillator and and excitable neuron might remain constant under changes of frequency in the oscillator; the mechanism is very robust and should work for a large class of relaxation oscillators, including standard models of neurons. This method has led to current work of Kopell on a lamprey–related problem for the regulation of phase lags between a pair of oscillators as the frequency is changed. Marder, Abbott and Kepler have produced a paper on "The effect of the electrical coupling on the frequency of a neuronal ocscillator, with the anti–intuitive answer that the coupling can lead to either an increase or a decrease in the network frequency. This work is motivated by a subnetwork of the STG consisting of an inherent oscillator and a follower cell with electrical coupling. Abbott, Kepler and Kopell plan next to look at a 3–cell subnetwork including the above two cells to try to understand the reasons for the apparantly conflicting excitatory and inhibitory connections, with experiments to be planned and done by the Marder lab.

III. Related mathematical work

Kopell and C. K.R.T. Jones of the University of Maryland have been doing foundational work related to singularly perturbed differential equations. For such equations, one can compute possible approximations to solutions by taking certain limits, but there is no comprehensive theory that guarantees that there are any solutions near such "approximations". Jones and Kopell have found techniques to develop such a theory for a large class of equations not previously covered. The theory gives more detailed information about nerve conduction equations and their stability than previous theories.

This work is not yet directly related to that in I and II. However, many of the equations associated with neurons and networks of neurons are singularly perturbed. Kopell feels that such foundational work is important to being able to analyze networks of neurons, such as subnetworks of the STG.

Laederich, who was supported for two years under the Center grant, received his Ph.D in June 1989 and is spending this year as a postdoctoral fellow at the Institute for Mathematics and its Applications at Minnesota. He was one of a very small number of fresh Ph.D.s accepted by the Institute. Several of his papers are enclosed.

IV. Other Activities

The collaborations have been carried out using a combination of telephone, E–Mail and visits. The Center held its third annual meeting at Ithaca July 7 – July 10 with 14 participants and intense interactions. We are now planning the meeting for this coming July.

The work of the Center members has been widely publicized though talks and posters. A poster of the work of Sigvardt, Williams, Kopell, Ermentrout and Remler was presented, as mentioned above, at two major meetings, as was the work of Marder's group. On the lamprey work alone, Kopell and Ermentrout gave at least twenty invited talks and Cohen gave five. The Center has also supported the activities of graduate students other than the ones named as members. At B.U. alone, it gave partial support to three other students who worked on projects related to tasks of the Center.

Manuscripts

1. G.B. Ermentrout and N. Kopell, Multiple pulse interactions and averaging in systems of coupled oscillators", submitted to J. Math Biol.

2. N. Kopell and G.B. Ermentrout, "On chains of oscillators forced at one end", preprint.

3. T.L. Williams, K.A. Sigvardt, N. Kopell, G.B. Ermentrout and M.Remler, "Forcing of coupled nonlinear oscillators: Studies of intersegmental coordination in the lamprey locomotor central pattern generator", submitted to J. Neurophysiol.

4. K.A. Sigvardt, T.H. Williams, N. Kopell and G.B. Ermentrout, "Forcing of non–linear oscillators: studies of intersegmental coordination in the lamprey locomotor central pattern generator" (abstract of the above), in Neural Mechanisms of Behavior, J. Erber, H. Menzel, H. Todt, eds. Stuttgart, 1989.

5. T.L. Williams, K.A. Sigvardt, N.Kopell and G.B. Ermentrout, "Intersegmental coordination in the locomotor spinal CPG:Theory and Experiment", Soc. for Neuroscience Abstr. 1989

6. S. Laederich and M. Levi, "Qualitative dynamics of planar chains", preprint

7. S. Laederich and M. Levi, "Invariant curves and time–dependent potentials", preprint.

8. S. Laederich, "Periodic solutions of nonlinear differential–difference equations", preprint.

9. S. Alford, K.A. Sigvardt, T.L. Williams, "GABAergic control of rhythmic activity in the presence of strychnine in the lamprey spinal cord", Brain Research, in press.

10. K.A. Sigvardt, "Modulations of properties of neurons underlying rhythmic movements in vertebrates", Seminars in Neuroscience, 1:55–65 (1989).

11. S. Alford and K. Sigvardt, "Excitatory neurotransmission activates voltage–dependent properties in neurons in spinal motor system of lamprey", J. Neurophys. 62:334–342 (1989).

12. A.H. Cohen, M.T. Baker and T.A. Dobrov, "Evidence for functional regeneration in the adult lamprey spinal cord following transection", Brain Research, 496: 368–372 (1989)

13. E. Marder and P. Meyrand, "Chemical modulation of oscillatory neural circuits", in Cellular and Neuronal Oscillators, J. Jacklet, ed., Marcel Dekker N.Y. pp317–338 (1989(

14. P.S. Dickenson and E. Marder, "Peptidergic modulation of a multi–oscillator system in the lobster. I. Activation of the cardiac sac rhythm by the neuropeptides proctolin and red pigment concentrating hormone", J. Neurophysiol., 61:833–884.

15. E. Marder and M.P. Nussbaum, "Peptidergic modulation of the motor pattern generators in the stomatogastric ganglion", in Perspectives in Neural Systems and Behavior", T.C. Carew and D. Kelley, eds., Alan Liss Inc, N.Y. pp73–91 (1989).

16. Weimann, J.M., Meyrand, P. and Marder, E. (1990) "Neurons that participate in several behaviors", In Wiese K., ed. Crustacean Pioneer Model Systems in Neurobiology, in press

17. Epstein, I.R. and Marder, E. (1990) " Modulation of a conditional neural oscilllator: A model describing the action of multiple modulatory substances", (submitted for publication)

18. Meyrand, P. and Marder, E. (1990) "Matching neural and muscle oscillators control by FMRFamide-like peptides", (submitted for publication)

19. Golowasch, J., Buchholtz, F., Epstein, I.R., and Marder, E. (1989) "Biophysical and theoretical characterization of the currents of crab stomatogastric ganglion neorons" Soc. Neoru. Abst. 15: 366

20. Weimann, J.M. and Marder, E. (1989) "Activation of the gastric rhythm of the crab stomatogastric ganglion by SDRNFLRFamide" Soc. Neuro. Abst. 15: 1047

21. Weimann, J.M., Meyrand, P., and Marder, E. (1989) "Neurons that participate in several behaviors" In: Erber, J., Menzel, R., Pfluger, H-J., and Todt, D., eds. Neural Mechanisms of Behavior Stuttgart, p.58